

ROLES FOR MODERN PLANT SYSTEMATICS IN DISCOVERY AND CONSERVATION OF FINE-SCALE BIODIVERSITY

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ABSTRACT

Systematic methods involving the use of DNA data and genealogical analysis have been widely applied to higher-level phylogenetic questions in plants but much less commonly to discovering plant lineages corresponding to minimal-rank taxa (i.e., species, subspecies, and varieties) or to refining plant classification at the finest levels. Recent research in the Jepson Herbarium integrating extensive field sampling, biosystematic data, and molecular phylogenetics provides examples from the California flora for assessing the value of modern systematic approaches as a means of discovering fine-scale plant diversity. Results have sometimes led to taxonomic changes at the levels most important for biodiversity assessment and have allowed resolution of systematic questions important to establishing conservation strategies. Angiosperm groups newly resolved with molecular data include both morphologically distinctive and morphologically cryptic lineages that have been previously treated within more broadly circumscribed species, subspecies, or varieties. Taxonomic recognition of such newly resolved lineages is often necessary if taxonomy is to reflect monophyletic groups and fine-scale units of biodiversity. To promote discovery, recognition, and conservation of plant lineages, systematists are advised to sample widely within minimal-rank taxa (including rare taxa) in the field and in herbaria, to consider previous taxonomies, to voucher all collections, to examine multiple lines of systematic evidence, and to publish taxonomic changes, including nomenclatural changes. Scientists involved in biodiversity management and conservation are advised to regard circumscriptions of all taxa as hypotheses of natural groups, to recognize that those hypotheses are subject to change, and to welcome taxonomic and nomenclatural changes that reflect an improved understanding of natural groups. Conservation biologists are urged to bear in mind that species or infraspecific taxa are not necessarily the minimal units of biodiversity. To conserve evolutionary lineages (and potential for future evolution), plant managers must seek to conserve representative populations of taxa from throughout their geographical and ecological distributions, must resist indiscriminate use of non-local germplasm in restoration efforts, and must consider cryptic biodiversity in regional conservation planning.

Systematics is fundamental to understanding of biodiversity. The most widely recognized organismal units of biodiversity, i.e., species, may not represent natural evolutionary groups or may not reflect the finest-scale natural groups that can be resolved and described by systematists. Modern systematic approaches that allow a genealogical perspective on biodiversity hold great promise as a means of achieving a refined taxonomy that better reflects evolutionary lineages of organisms throughout the tree of life (e.g., Angiosperm Phylogeny Group 1998). To date, modern systematic approaches to resolving evolutionary relationships have been applied by plant systematists mostly to questions concerning groups of recognized species or higher-level taxa (see Soltis et al. 1998). Recent studies of higher-level plant phylogeny have yielded insights into broad-scale evolutionary and biogeographic patterns that are directly relevant to biodiversity assessment and prioritization of conservation efforts (e.g., Vane-Wright et al. 1991; Mishler 1995; Faith 1996; reviewed by Soltis and Gitzendanner 1998).

Modern systematic methods have been applied less commonly to testing the naturalness of mini-

mal-rank taxa (i.e., species, subspecies, and varieties), which are of most immediate concern to conservation biologists, ecologists, and floristicians (e.g., Rieseberg et al. 1988; see Soltis et al. 1992). Studies of phylogeographic diversity—fine-scale, geographically structured evolutionary lineages corresponding to “Evolutionarily Significant Units” (*sensu* Moritz 1994)—also have been extremely limited for plants (e.g., Fujii 1997; Soltis et al. 1997; Olsen and Schaal 1999; Tremblay and Schoen 1999; Shaw 2000; also see Schaal et al. 1998; Schaal and Olsen 2000), especially by comparison with the rich literature on animal phylogeography (reviewed by Avise 2000). As noted by Moritz (1995, 1999) and Coates (2000), conserving independently evolving sets of populations not only preserves biodiversity but also may be the best strategy for conserving the potential for future evolution. On a regional scale, refined understanding of phylogeographic patterns across organismal groups may allow for improved resolution of biodiversity hot-spots and identification of critical areas for conservation attention (see Moritz and Faith 1998).

In this paper, I present examples of previously

undetected diversity resolved from studies of the California flora conducted in the Jepson Herbarium. These studies illustrate both the potential and the proven value of applying modern systematic methods to discovery of fine-scale plant diversity and to refining classifications of minimal-rank plant taxa. Finally, I make general recommendations for how systematists and other biodiversity scientists and planners may promote discovery and conservation of plant diversity.

EXPLORATION IN THE FIELD AND LABORATORY

Well-focused field exploration (see Ertter 2000a) and detailed systematic analysis are complementary components of an effective strategy for discovering plant diversity. As reviewed by Ertter (2000b), botanical field exploration in western North America, often by non-academic professionals and amateurs, has been a continuing source of floristic novelties. Modern systematic approaches can contribute greatly to the process of discovery by offering a rigorous means of resolving the systematic status of recently discovered plant populations. For example, DNA sequence variation may clarify whether phenotypically unusual populations or sets of populations belong within previously described, minimal-rank taxa or represent undescribed evolutionary groups (e.g., Baldwin 1999a). Data from DNA also may allow confident taxonomic placement of newly discovered plants that are evidently distinct from any described minimal-rank taxon but of uncertain position (e.g., Boyd and Ross 1997). Conversely, fine-scale systematic studies depend on extensive field sampling across the geographical and ecological distribution of taxa for assessing naturalness of groups and detecting any unrecognized diversity within a group. Phylogeographic studies have demonstrated the potential for discovery of geographically distinct, and often morphologically cryptic, evolutionary lineages within both widespread and narrowly distributed species (see Soltis et al. 1997; Moritz 1999; Avise 2000; Riddle et al. 2000). Systematic studies and floristic surveys that involve extensive geographic sampling of widespread taxa as well as locally restricted taxa are therefore advisable to maximize the potential for discovering unrecognized plant diversity.

The prospect for floristic discoveries to result from more detailed systematic analyses of western North American plant groups appears great. Young lineages, which account for much of the endemic plant diversity in western North America, e.g., California (Raven and Axelrod 1978), can be expected to exhibit mosaic or cryptic phenotypic variation from minimal divergence, differential sorting of ancestral polymorphism through descendant lineages (see Maddison 1995), or hybridization (see Arnold 1997). Climatic and geologic upheaval and extensive species turnover seen in the plant fossil record during the mid to late Cenozoic in western North

America has been associated with the rise of diverse lineages of annuals and perennials that are largely or entirely restricted to the region (Axelrod 1992; Graham 1999). The high degree of endemism, ca. 50% of species, in the California Floristic Province, i.e., the Mediterranean-climatic region of western North America (Raven and Axelrod 1978), largely reflects high diversity in neoendemic groups wherein often only minimal morphological divergence has occurred between evolutionary lineages.

Systematists in California and elsewhere in western North America have long appreciated the complexity of the regional flora and the need for in-depth evolutionary investigations to reveal natural units of biodiversity. The San Francisco Bay Area botanists Harvey Monroe Hall, Ernest Babcock, G. Ledyard Stebbins, Jens Clausen, David Keck, William Hiesey, and others pioneered the incorporation of genetic principles and experimental approaches into systematics in a highly successful effort to resolve evolutionary lineages and understand complex patterns of variation in the California flora (e.g., Babcock and Hall 1924; Stebbins 1950; Clausen 1951; also see Smocovitis 1997). Subsequent developments in systematics now allow even more progress in discriminating natural plant groups and refining the taxonomy of western North American plants.

Advances in phylogenetic theory and methodology, together with the development of accessible high-speed computers, now permit simultaneous analysis of large numbers of variable characters to produce rigorous hypotheses of evolutionary relationships within plant groups, as well as estimates of support for resolved lineages (see Swofford et al. 1996). Character changes (resulting from mutations) allow diagnosis of monophyletic groups (=evolutionary lineages or clades), the most natural groups recognized by systematists (Hennig 1966; see Mishler 1995, 2000a, b)—plants belonging to monophyletic groups are more closely related to one another than to plants in other groups. Access to an ever-increasing number of macromolecular characters from DNA sequences has enhanced the prospects for systematists to attain fine-grained, robust resolution of evolutionary lineages (see Hillis et al. 1996; Soltis et al. 1998).

EXAMPLES OF RECENT PLANT DISCOVERIES FROM SYSTEMATIC STUDIES

To illustrate the utility of modern systematic methods for discovery of plant groups, I present below some examples from research conducted in my lab at the Jepson Herbarium, principally on Californian angiosperm lineages. Although categorization of the examples is somewhat artificial, three general types of problems are addressed: confusing variation within taxa, resolution of cryptic biodiversity, and questionably distinct rare taxa.

I. *Variation within taxa reexamined.* The first category of examples comprises groups wherein morphological variation within a taxon was of uncertain systematic significance until phylogenetic studies were undertaken.

Deinandra bacigalupii: A narrow endemic misplaced in a widespread species.—*Deinandra* is a species-rich genus of tarweeds (Madiinae, Compositae) reinstated for members of *Hemizonia* sensu Keck (1959) that are most closely related to *Holocarpha* (Baldwin 1999b). Until 1999, an ca. 8-rayed *Deinandra* from alkaline meadows in the Livermore Valley, California, was treated within *D. [Hemizonia] increscens* subsp. *increscens*, a mostly coastal taxon known otherwise from Santa Barbara County to Monterey County, California (Tanowitz 1982), more than 75 km south of Livermore Valley. Morphologically, the Livermore Valley tarweed is highly similar to *D. increscens* except in anther color and pappus characteristics. Robert F. Hoover collected and left unidentified to species the Livermore Valley tarweed as early as 1966. Rimo Bacigalupi annotated the UC accession of the first known collection (by Hoover) as not matching any published species of *Hemizonia*.

Dean Kelch and Robert Preston independently collected the Livermore Valley tarweed in the 1990's and brought specimens to me with concerns that the plant was not identifiable with *The Jepson Manual: Higher Plants of California* (Hickman 1993). The characteristics of yellow to brownish, rather than "black" (i.e., dark purple), anthers in the Livermore Valley plants was in conflict with placement in *Deinandra [Hemizonia] increscens* and ray laminae of the plants were much too short for *D. [Hemizonia] pallida*. Further examination of the plants in comparison with other deinandras revealed that the pappus was much shorter and more irregular than in other populations then assigned to *D. increscens* (Baldwin 1999a). Chromosome counts of the Livermore Valley tarweed of $2n = 12$ II, the modal chromosome number in *Deinandra* (as in *D. increscens*), were inconclusive about relationships of the plants (Baldwin 1999a).

Results of phylogenetic analysis of nuclear ribosomal DNA (rDNA) sequence data, in concert with the morphological evidence, led me to conclude that the Livermore Valley tarweed is not a member of *Deinandra increscens* or any other previously recognized species of *Deinandra* (Fig. 1; Baldwin 1999a). Representatives of the two most divergent groups of *D. increscens*, i.e., *D. i.* subsp. *increscens* and *D. i.* subsp. *villosa*, were resolved as a well-supported monophyletic group to the exclusion of representatives of the other six recognized species of the "northern lineage" of *Deinandra* and the Livermore Valley tarweed. The Livermore Valley tarweed does not appear to be of recent hybrid origin based on 10 unambiguous rDNA mutations not shared with any other sampled

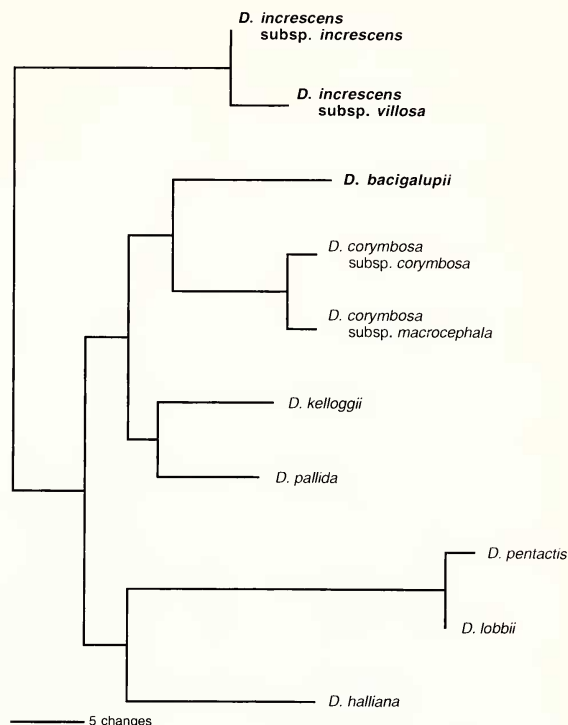


FIG. 1. The most parsimonious tree from phylogenetic analysis of 18S-26S nuclear ribosomal DNA sequences of the external and internal transcribed spacers for the northern lineage of *Deinandra* (Compositae—Madiinae; Baldwin unpublished data). The outgroup (*D. minthornii*) used for rooting the tree is not shown, nor are tree statistics and support values (to be published elsewhere). Note the extensive divergence of the Livermore Valley tarweed (*D. bacigalupii*) from other representatives of *Deinandra* and the remote phylogenetic position of *D. bacigalupii* from *D. increscens*, the species in which the Livermore Valley tarweed was earlier treated.

plants from the "northern lineage" of *Deinandra* (Baldwin, unpublished data).

Evidence from DNA substantially augmented morphological evidence for distinctiveness of the Livermore Valley tarweed from *D. increscens*. Recognition of *D. bacigalupii* as distinct from *D. increscens* improves our understanding of diversity in *Deinandra* and rare plants in general in the Springtown wetlands area near Livermore, California. *Deinandra bacigalupii* has been regarded as an example of a plant species that was discovered "in front of the bulldozer" (Erter 2000b), i.e., that came close to being driven to extinction prior to being recognized as distinct.

Layia gaillardoides: Interpopulational variation of phylogenetic significance.—*Layia gaillardoides*, the woodland layia, has been regarded as an example of a species displaying substantial morphological variation among populations (Clausen 1951). Ray laminae may be uniformly deep yellow or have white, greenish, or pale yellow apices de-

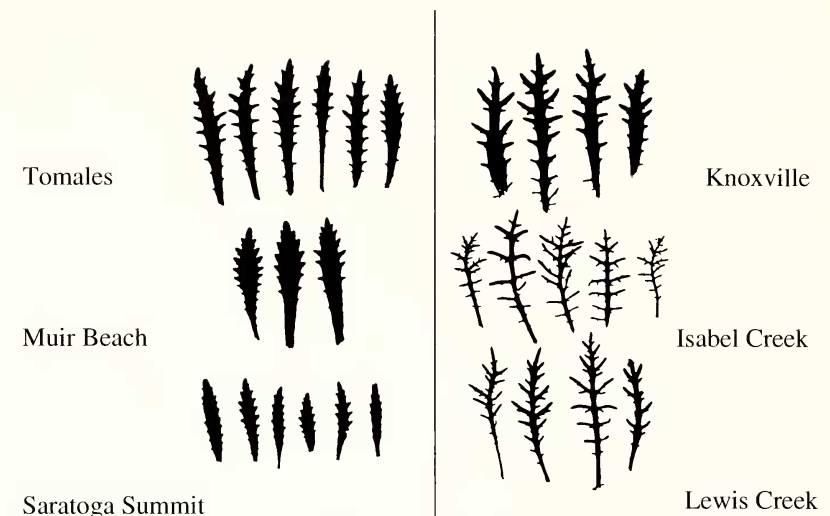


FIG. 2. Basal leaf variation in the woodland layia, *Layia gaillardoides* (modified from Clausen 1951). Leaves separated by the vertical line correspond to outer (left) and inner (right) Coast Range populations in central and northern California. The populational differences shown here correspond to variation across three divergent molecular lineages that do not appear to constitute a natural group (Baldwin, unpublished data).

pending on the population examined. Clausen (1951) noted that inner and outer Coast Range populations differ in stem thickness and degree of lobing of the basal leaves, characteristics that he concluded were heritable and ecologically significant (Fig. 2).

Phylogenetic analysis of *Layia* has revealed evidence that *L. gaillardoides* as circumscribed at present represents an unnatural group (Baldwin, unpublished data). Populations shown earlier by Clausen to be morphologically distinct constitute three distinct lineages that apparently are not most closely related to one another. Two lineages of *L. gaillardoides* are more closely related to *L. carnosa*, *L. hieracioides*, and *L. septentrionalis* than to a third lineage of *L. gaillardoides*. Each of the groups resolved within *L. gaillardoides* is well-supported by unique rDNA mutations, and relationships among the lineages and related species are likewise robust based on rDNA data. Evolutionary lineages within the woodland layia conform to a typical phylogeographic pattern except that the natural groups within *L. gaillardoides* do not constitute a clade and instead represent a paraphyletic or (conceivably) polyphyletic group (see Riddle et al. 2000 for similar examples). Recognition that *L. gaillardoides* has been circumscribed too broadly and comprises multiple natural groups, each probably warranting taxonomic distinction, may be an important conservation concern given the evidently scattered distribution and small size of woodland layia populations. Sampling of additional populations and DNA regions is now underway to resolve the precise delimitation of each evolutionary lineage within *L. gaillardoides* s. lat. prior to describing segregate taxa.

Lessingia: Problems in species and varietal circumscriptions in the "yellow group."—Systematic investigations by Markos (2000; also see Markos and Baldwin 2001) revealed an outstanding example of misinterpreted morphological variation in another lineage of annuals in the California Compositae, namely, in the "yellow group" of *Lessingia* (Astereae). Markos (2000) found that annuals in *Lessingia* constitute two major lineages that differ in disc corolla coloration—a pink-to-white-flowered lineage and a yellow-flowered lineage. Within the "yellow group," Markos (2000) used morphological and molecular data to resolve three major natural groups that span the boundaries of widely recognized species and varieties.

Markos (2000) found that different representatives of each of three taxa (*Lessingia glandulifera*, *L. glandulifera* var. *glandulifera*, and *L. lemmonii*) belong to different major lineages within the "yellow group." Morphologically, differences in shape of the style-branch appendages and presence or absence of a maroon band in the corolla throat diagnose the three primary lineages of yellow-flowered lessingias. Markos (2000) concluded from her phylogenetic data that the accepted taxonomy of *Lessingia* underrepresents the actual biodiversity of the group and warrants substantial revision (S. Markos, in prep.).

II. *Cryptic biodiversity*. Modern systematic methods have promising potential for allowing discovery of natural plant groups that are morphologically indistinguishable (or nearly so) from one another but may be geographically or ecologically distinct. As noted above, lineage diversity across the geographic distribution of a morphological or

biological species, i.e., phylogeographic diversity, has been widely reported in vertebrates but has not been extensively studied in plants (see Soltis et al. 1997; Avise 2000; Schaal and Olsen 2000). In Californian groups of annuals, members of my lab have found various examples of cryptic diversity associated with geography. Two examples are particularly important for illustrating groups that are not only morphologically cryptic but, based on multiple lines of evidence, must be recognized as distinct taxa because the well-supported but morphologically indistinct lineages are evidently not most closely related to one another.

Downingia yina.—Schultheis (2000) examined relationships throughout *Downingia* (Lobeliaceae) with special attention to a lineage corresponding to three morphological species: *D. bacigalupii*, *D. elegans* and *D. yina*. Earlier work by Weiler (1962) and Foster (1972) established that *D. yina* is cytologically highly unusual, with a broad dysploid series of chromosome numbers, i.e., $2n = 6, 8, 10$, and 12 II. Chromosome "races" of *D. yina* are mostly geographically distinct but could not be distinguished reliably on the basis of morphology using multivariate analyses and other approaches (Schultheis 2000).

Schultheis (2000) extensively sampled *D. bacigalupii*, *D. elegans*, and *D. yina* throughout their geographic ranges in an attempt to discern the evolutionary significance of chromosomal variation in the group. She found strong phylogenetic signals from sequences of both chloroplast DNA (cpDNA) and nuclear rDNA for three major lineages with cytological and geographic integrity that each include populations of *D. yina*. One lineage corresponds to populations west of the Cascade Range, all with chromosome numbers of $2n = 6, 8$, or 10 II, i.e., *D. elegans* ($2n = 10$ II) and populations of *D. yina* with $2n = 6, 8$, or 10 II. The second lineage corresponds to a pocket in the southern Cascade Range of Oregon wherein populations of *D. yina* with $2n = 10$ II are found. The third lineage corresponds to populations east of the Cascades, with $2n = 12$ II, i.e., *D. bacigalupii* and *D. yina*.

Schultheis (2000) concluded that the three well-supported evolutionary lineages in *D. yina* warrant taxonomic recognition despite being only cryptically distinct morphologically. Congruence between two lines of molecular data leave minimal doubt that *D. yina* represents an example of divergent evolutionary lineages that remained morphologically static while closely related lineages (corresponding to *D. bacigalupii* and *D. elegans*) underwent considerable morphological change. Differences among the three major groups of *D. yina* in geographic distribution and nuclear genomic arrangements conceivably extend to physiological differences of fundamental importance to survivorship in distinct ecological settings.

Lasthenia californica.—The goldfield genus *Lasthenia* (Compositae) has been the subject of a re-

cent molecular phylogenetic study by Chan (2000), who sampled widely across populations of each taxon recognized by Ornduff (1966, 1993). Chan found strong evidence from cpDNA and nuclear rDNA sequences for morphologically cryptic lineages in *L. californica*, the most widespread species recognized by Ornduff (1993).

Chan's (2000) cpDNA and nuclear rDNA data led him to propose the hypothesis that one set of populations of *L. californica sensu* Ornduff (1993) is most closely related to the outer coastal, endemic Californian taxa *L. macrantha* subsp. *macrantha* and *L. m.* subsp. *bakeri*. Chan concluded that the three taxa constitute a well-supported group exclusive of the Pacific Northwest endemic *L. macrantha* subsp. *prisca* and other populations of *L. californica sensu* Ornduff (1993). Chan (2000) also found that the two lineages corresponding to *L. californica sensu* Ornduff (1993) have somewhat distinct (but overlapping) geographic distributions and minor pappus differences, although some individuals of both groups are epappose and cannot be reliably distinguished morphologically. *Lasthenia californica sensu* Ornduff (1993) appears to represent another example, parallel to *Downingia yina*, of lineages that do not constitute a natural group but have remained morphologically similar while related lineages have undergone substantial morphological change.

Taxonomic recognition of cryptic plant groups.—Morphologically indistinct evolutionary groups such as the two examples discussed above (within *Downingia yina* and *Lasthenia californica*) present a special challenge to plant systematists and the botanical community. Cryptically distinct lineages that together constitute a monophyletic group may or may not be viewed as warranting taxonomic recognition. In the interests of accurate biodiversity assessment (which typically relies on taxa as units), I suggest that cryptic groups that are: (1) well-supported by different lines of molecular or other evidence, and (2) geographically or ecologically distinct should be recognized as taxonomically distinct. Well-supported, cryptically-distinct groups that are not even most closely related to one another (e.g., groups in *D. yina* and in *L. californica*) leave systematists committed to natural classification with no choices other than to recognize the cryptic groups as taxonomically distinct or to treat all members of the minimal monophyletic group encompassing the cryptic lineages and the related group(s) as a minimal-rank taxon. I believe that the second option is undesirable because it underrepresents biodiversity.

Practicality of classification is a concern for plant systematists and other botanists, especially for those faced with accurately identifying plant taxa with minimal time and resources. A system of classification that does not allow some plant taxa to be identified on the basis of macroscopic morphological characteristics alone generally has been resisted

by vascular plant systematists (but not bryologists or other botanists). Insofar as geography or habitat characteristics often aid identification of cryptic lineages, practical problems arising from giving formal taxonomic status to morphologically indistinguishable groups may be limited. Eventually, advances in DNA analysis and computer technology may trivialize the process of screening for diagnostic genetic markers, even in the field, thereby allowing botanists to be less reliant on morphological characteristics for plant identification. I recognize, however, that for plant groups wherein morphology has evolved even faster than DNA sequences in commonly examined, rapidly-evolving gene regions, e.g., in some examples of insular adaptive radiation (see Baldwin et al. 1998), morphology may provide a finer-scale perspective on evolutionary lineages than most easily obtained DNA data.

Strict adherence to a criterion of macroscopic diagnosability for all vascular plant taxa places unacceptable and unnatural limits on the information content of our taxonomy and potentially jeopardizes important segments of biodiversity because of a human bias toward recognizing only what can be seen with minimally-assisted human eyesight. From a biological standpoint, cryptic differences between plant groups, e.g., in characters associated with ecophysiology, can be more important to the integrity and fitness of plant groups than differences that humans can perceive visually. From a conservation perspective, taxonomic recognition of cryptically distinct natural groups may be important to ensure their legal protection (e.g., only formally-named plant lineages are eligible for protection under the U.S. Endangered Species Act). Taxonomic status for cryptic groups also may help to ensure their protection from misguided restoration efforts that result in combining germplasm from different evolutionary lineages treated within the same minimal-rank taxon, with consequent loss of lineage integrity and possible outbreeding depression (see Moritz 1999). From a more general perspective, adherence to the belief that plant systematics is a science that seeks to discern real entities of nature, i.e., evolutionary groups, dictates that plant taxonomy should reflect rigorous hypotheses of relationship rather than convenient but artificial or oversimplistic assemblages. Based on available evidence, I suspect that widespread recognition of cryptic taxa would result in only a modest refinement, not a major overhaul, of plant taxonomy.

III. Conservation prioritization. Mishler (1995) and others have discussed the potential value of phylogenetic data on the age and position of lineages for prioritizing conservation efforts (reviewed by Soltis and Gitzendanner 1998). On an even more fundamental level, modern systematic data can help to resolve whether rare taxa of questionable naturalness truly represent evolutionary lineages worthy of conservation attention and re-

sources. Skinner et al. (1995) identified over 150 examples of rare, minimal-rank taxa of Californian vascular plants that needed systematic attention. The two rare taxa discussed below are examples of groups that were studied systematically in part to determine whether they warrant continued recognition and, for *Blepharizonia*, to determine whether gene flow between species represents a conservation concern.

Blepharizonia plumosa: Rare species or minor morphological variant?—Baldwin et al. (2001) examined biosystematic and phylogenetic data for *Blepharizonia* to assess whether the common big tarweed, *B. plumosa* subsp. *viscida*, warrants taxonomic distinction from the rare big tarweed, *B. plumosa* subsp. *plumosa*. Keck (1959) regarded the two taxa as allopatric but recent field work by Robert Preston established that the two taxa are mosaically sympatric in the northern Mt. Hamilton Range, California, where Baldwin et al. (2001) sampled the big tarweeds for crossing and molecular studies. Phylogenetic analysis of rDNA sequence data yielded evidence for ancient divergence between the two taxa of *Blepharizonia* relative to timing of divergence between taxa in the sister-genus, *Hemizonia* (Fig. 3). Low interfertility of artificial hybrids corroborated phylogenetic evidence for greater divergence between the big tarweed taxa than implied by Keck's (1959) taxonomy.

Baldwin et al. (2001) concluded that the two taxa of *Blepharizonia* should continue to be recognized and warrant treatment as separate species, *B. laxa* (= *B. plumosa* subsp. *viscida*) and *B. plumosa* (= *B. plumosa* subsp. *plumosa*). Baldwin et al. (2001) also concluded from DNA and artificial hybridization data that natural hybridization between *B. laxa* and *B. plumosa* probably does not pose a threat to the continued existence of the rare big tarweed, *B. plumosa*. Preliminary evidence for phylogeographic diversity uncovered within the rare *B. plumosa* (Baldwin et al. 2001) should serve as a caution against any conceivable restoration efforts that involve moving germplasm of *B. plumosa* between populations (especially north or south of the Livermore Valley), at least until continuing studies of lineage diversity in *Blepharizonia* are completed.

Sidalcea keckii: A minor variant of *S. diploscypha* or a distinct, rare lineage?—Phylogenetic studies of *Sidalcea* (Malvaceae) by Andreassen (in prep.; see also Andreassen and Baldwin, 2001) helped to clarify evolutionary lineages in the genus, a group previously regarded as highly variable, taxonomically difficult, and in need of systematic attention (Hill 1993). Among the issues of conservation concern examined by Andreassen was the evolutionary status of *S. keckii*, a narrowly endemic species from Tulare County, California, long thought to be extinct until rediscovered in 1992 (see Skinner and Pavlik 1994). Assigning conservation priority to *S. keckii* has been complicated by uncertainty about

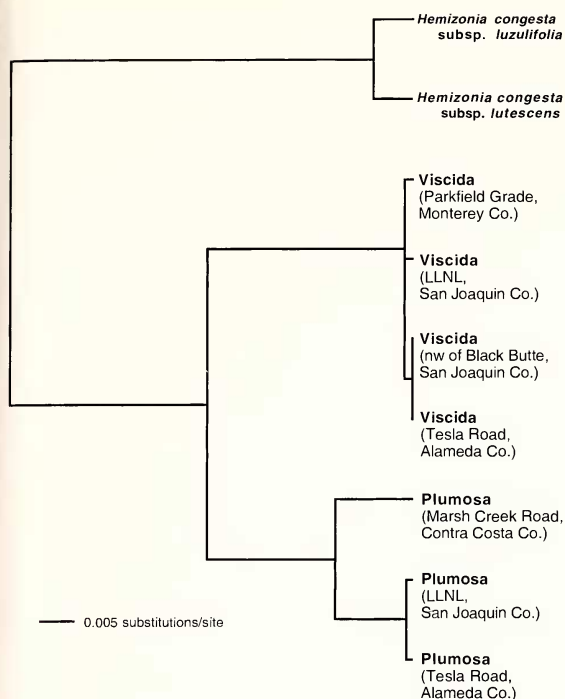


FIG. 3. Chronogram of one of two maximally parsimonious trees from phylogenetic analysis of nuclear ribosomal DNA sequences of *Blepharizonia* and *Hemizonia* (modified from Baldwin et al. 2001). Branch lengths were optimized by maximum-likelihood to conform to an hypothesis of evolutionary rate constancy, which could not be rejected using a tree-wide likelihood-ratio test. Note the extensive divergence between the two, minimally interfertile, mosaically sympatric taxa of *Blepharizonia* relative to divergence between the two representatives of *Hemizonia*. Biosystematic and phylogenetic data led Baldwin et al. (2001) to conclude that the two taxa of *Blepharizonia* each correspond to natural groups that warrant treatment as distinct species. Abbreviations: Plumosa = *B. plumosa sensu stricto* [= *B. plumosa* subsp. *plumosa*]; Viscida = *B. laxa* [= *B. plumosa* subsp. *viscida*]. See Baldwin et al. (2001) for tree statistics and support values.

distinctiveness of the species from the morphologically similar, widespread species *S. diploscypha*.

Andreasen (in prep.; see also Andreasen and Baldwin, 2001) sampled both species in a genus-wide phylogenetic analysis of rDNA spacer sequences in *Sidalcea*. She found that *S. diploscypha* and *S. keckii* were most closely related to one another, as expected, but that representatives of each species constituted highly divergent lineages. Based on her findings, Andreasen concluded that *S. keckii* is worthy of continued taxonomic recognition and conservation attention.

RECOMMENDATIONS FOR SYSTEMATIC STUDIES

To promote further progress by systematists in the discovery of plant diversity corresponding to minimal-rank taxa and in the refinement of plant

classification at the lowest taxonomic levels, the following recommendations are presented for planning systematic studies:

- *Sample widely within accepted taxa.* To test taxonomic hypotheses and to detect cryptic lineage diversity, sampling within taxa across the range of phenotypic variation and across the geographical and ecological distribution has been productive (see above). Examining only one exemplar per taxon cannot reveal hidden diversity or problems in circumscription at the taxonomic level of sampling.
- *Study herbarium collections.* Apart from yielding valuable data on morphological, ecological, and geographic variation within minimal-rank taxa, studies of herbarium specimens may reveal undescribed diversity more readily than new field exploration. Feasibility of extracting sufficient DNA for genetic analyses from small fragments of dried plant material may allow both morphological and molecular characterization of new species discovered in herbaria (e.g., Vargas et al. 1998).
- *Take seriously the old taxonomic literature.* A sampling focus on taxa recognized only in the most recent taxonomic revision of a plant group may ensure a repeat of errors made in that systematic treatment, especially if sampling within taxa is minimal. In addition to taking a fresh look at variation within a group, systematists may find that taxa no longer recognized in modern treatments represent evolutionary lineages warranting recognition (e.g., Chan 2000).
- *Voucher all specimens examined.* Vouchering specimens for systematic studies of groups corresponding to minimal-rank taxa is perhaps even more essential than for studies at higher taxonomic levels to ensure that the identities of sampled plants are not misinterpreted by others. Documentation of detailed collection data is also critical for studies involving fine-scale sampling within minimal-rank taxa (see Huber 1998).
- *Examine multiple lines of systematic evidence.* A single line of systematic evidence (e.g., one gene) can be potentially misleading about relationships within a group (see Wendel and Doyle 1998). Lineage sorting and hybridization are more likely to affect evolutionary patterns in young plant groups than in old lineages. Examining multiple, unlinked gene regions or molecular and other lines of data (e.g., morphology or cytology) should increase the likelihood of achieving an accurate understanding of natural plant groups.
- *Sample the rare taxa.* The potential value to conservation biology of gaining additional systematic data on rare plants makes the efforts required to sample rare taxa worthwhile. Most modern molecular systematic methods involve use of the polymerase chain reaction (PCR), which requires

only minimal DNA (see Hillis et al. 1996). Molecular data from rare plants can be obtained from minute amounts of fresh or dried (e.g., herbarium) tissue without impacting populations or significantly damaging voucher specimens.

- *Study biological characteristics of the plants.* Including an experimental biosystematic component (e.g., from artificial hybridizations or common gardens) and field component (e.g., pollination ecology, demography) in modern systematic studies can yield valuable biological data for resolving fine-scale diversity within a group and may lead to insights into evolutionary processes affecting diversification (see Baldwin 1995). Studies of population-genetic structure within lineages can provide critical biological data for resolving microevolutionary dynamics of populations and for refining conservation strategies (e.g., Bushakra et al. 1999).
- *Communicate with other field botanists.* Close communication and cooperation with professional and amateur field botanists is especially valuable for promoting discovery and conservation of plant diversity. The reciprocal flow of knowledge that can develop between systematists and other field-immersed plant biologists enriches botany in general and can lead to a more intensive, well-focused effort toward detecting and conserving diversity than would be otherwise possible (see Ertter 2000a, b).
- *Publish findings and follow through on taxonomic changes.* Other biologists, especially those involved in biodiversity assessment and conservation (e.g., Skinner and Pavlik 1994), rely on formal taxonomic treatments and other publications by the systematic community. Translating pertinent results of systematic studies into taxonomic changes is a potentially tedious but necessary step to ensure that newly discovered evolutionary lineages and new understanding of the circumscriptions and positions of monophyletic plant groups in general are recognized by others.

RECOMMENDATIONS TO THE CONSERVATION COMMUNITY

Based on the evidence from phylogenetic studies that circumscriptions of some minimal-rank taxa misrepresent or under-represent biodiversity, I suggest that the following recommendations be adopted by the conservation community in the interests of preventing loss of natural plant groups:

- *Regard taxa as hypotheses of natural groups subject to change.* Some refinements to our understanding of the composition and position of natural plant groups are inevitable and desirable to ensure that conservation efforts are well directed.
- *Accept and encourage taxonomic changes based on solid evidence of natural groups.* Although taxonomic changes create difficulties in data-

base management and communication, changes that reflect an improved understanding of natural groups are valuable and worth adopting. From a conservation perspective, names are expendable; natural plant groups are irreplaceable.

- *Bear in mind that recognized species or infra-specific taxa are not necessarily minimal units of biodiversity.* As noted above, unrecognized, evolutionarily distinct lineages may exist within a species, subspecies, or variety (also see Soltis and Gitzendanner 1998). Research efforts to discern any undetected diversity within minimal-rank plant taxa using modern systematic approaches (e.g., phylogeographic studies) have been minimal (see above). Available data suggest that cryptic lineages often show some degree of geographic distinction (see Avise 2000). Efforts to protect taxa throughout their geographical and ecological ranges are therefore warranted not only to ensure survival of locally adapted populations and overall allelic diversity within a group (Endler 1977; Chesser 1983) but also to preserve potentially distinct evolutionary lineages.
- *Resist proposals to use non-local germplasm indiscriminately in restoration efforts.* Use of non-local germplasm in restoration efforts may result in extensive hybridization between evolutionarily distinct but cryptic lineages and consequent loss of biodiversity (see Storfer 1999). This concern is especially important given the increasing prevalence of mitigation efforts seeking to augment rare plant populations in protected areas with propagules or mature plants translocated from other populations slated for destruction. The well-intentioned practice of augmentation may be justifiable to prevent or overcome inbreeding depression, e.g., if the populations involved are remnants of a more continuous metapopulation fragmented by human-related activities or if geneological and population genetic data indicate that declining populations are of a common regional lineage and share similar genetic structure (see Moritz 1999). Indiscriminate translocation of plants from one population to another has potential to do much harm to biodiversity and to our prospects for understanding the evolution or population-genetic structure of natural plant populations.

In the absence of geneological and population-genetic data, proposals for augmentation of natural populations with non-local seed should be viewed with the same skepticism as the universally objectionable idea of intermixing germplasm from unquestionably distinct but interfertile, naturally allopatric species. Even if the populations to be intermixed do not represent highly divergent evolutionary lineages, potential still exists for outbreeding depression from loss of local adaptation or breakdown of co-adapted gene complexes (see Templeton 1986; Slatkin 1987;

Moritz 1999; Storfer 1999). Planting of wild-flowers along roads and highways is another widespread practice with similar potential for reducing biodiversity and confounding scientific investigation of natural plant populations.

- *Consider cryptic biodiversity in conservation planning.* Even if systematists decline to recognize cryptic lineages as taxa, conservationists can plan for preservation of cryptic groups in the interests of preserving unnamed, as well as named, biodiversity. Under the U.S. Endangered Species Act, evolutionarily significant but morphologically indistinct and unnamed lineages of vertebrates are eligible for protection; similar protection for cryptic plant groups may be possible to achieve. Geographical and ecological criteria have been used effectively for recognizing cryptic vertebrate lineages (e.g., salmonids) and also may be useful for identifying various cryptic plant groups.

CONCLUSIONS

The potential for modern systematics to play an important role in the discovery and conservation of fine-scale plant biodiversity is enormous and mostly untapped. The movement of systematics toward use of molecular and phylogenetic methods has been perceived by some botanists as an alarming diversion from the urgent business of finding and describing previously undetected and, usually, endangered plant diversity ("fiddling while Rome burns"). I suggest that the use of modern systematic approaches, far from posing a threat to advancing our knowledge of fine-scale biodiversity, can be an invaluable means of achieving rapid progress in the discovery and conservation of plant lineages.

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